

GENERAL NOTES

Behavioral implications of aberrant song of a Red-eyed Vireo.—In studies of avian social behavior, song (or other relevant stimuli, *sensu* Tinbergen [The Study of Instinct, The Clarendon Press, Oxford, England, 1951]) is often taken to be prerequisite to potential pairing or territorial defense. Playback experiments have been used to identify the aspects of a species' song conveying specific sorts of information, e.g., the identity and condition of the species and/or individual singer, crucial to the performance of these social activities (Thompson, Anim. Behav. 17:658-663, 1969; Emlen, Z. Tierpsychol. 28:241-246, 1971; Goldman, Auk 90:106-113, 1974; Fletcher and Smith, Auk 95:338-347, 1978; and others). Some recent theories of evolution of aspects of mating systems and use of space hold that social signals may play an evolutionary pace-setting role (Wilson, Sociobiology: The New Synthesis, Harvard Univ. Press, Cambridge, Massachusetts, 1975). This implies that certain social signals are not only sufficient, but necessary for an individual to defend a territory or obtain and keep a mate. To test whether the performance of specific species-typical social activities is necessary as well as sufficient would require experimental subjects occurring in natural field conditions, which were deficient in the social signal of interest.

The primary song of the Red-eyed Vireo (*Vireo olivaceus*) is structurally diverse and complex (Lemon, Can. J. Zool. 49:847-854, 1971; Rice, Anim. Behav. 26:527-549, 1978a) and plays an important role in natural behavioral interactions among conspecifics, including territorial defense and pair formation and maintenance (Lawrence, Can. Field-Nat. 69:47-87, 1953; Rice 1978a). Playback of its species-typical song elicits responses from territory holders that are qualitatively and quantitatively similar to behaviors seen in natural encounters (Rice 1978a; Rice, Anim. Behav. 26:550-561, 1978b).

In June 1973 I discovered a Red-eyed Vireo consistently singing a song unrecognizable to me as belonging to that species. Dr. Jon Barlow, who has recorded songs of Red-eyed Vireos throughout the range of the species, also heard this bird sing, and thought the song was grossly aberrant. Although Red-eyed Vireos occasionally mimic other species (James, Can. J. Zool. 54:1223-1226, 1976), the song did not sound like that of any other bird. Analysis of the behavioral interactions of this aberrantly singing bird provides a natural experiment on the necessity of species-typical song for successful pair formation and maintenance and territoriality in Red-eyed Vireos.

Methods.—My study area was in Kap-Kig-Iwan Park, 1.6 km south of Englehart, Ontario. The habitat comprises a forest of predominantly trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) with an understory of speckled alder (*Alnus rugosa*) and beaked hazelnut (*Corylus cornuta*). A detailed description of the study area is given in Rice (Ecology 59:526-538, 1978c).

Behavioral interactions of Red-eyed Vireos and the procedure used in playback experiments are described in Rice (1978a). Briefly, experiments consisted of a 2-min pre-test period, followed by 2-min playback of song of the aberrant vireo, and then a 2-min post-test period. After a 10-min inter-trial interval the 3 periods were repeated, this time using normal song to provide a measure of the readiness of the subject to respond to a normal stimulus (Tinbergen 1951). During each 2-min period 17 variables were measured, covering aspects of rate, form and latency of song, as well as closeness and latency of approach to the speaker. These data were combined multivariately into a single response intensity score (Rice 1978b). For each experiment I present the scores for each period. To maximize precision, data from different subjects were not pooled. An instance of a test or post-test score being higher than the pre-test score is taken as possible evidence of a response to the song played during the test.

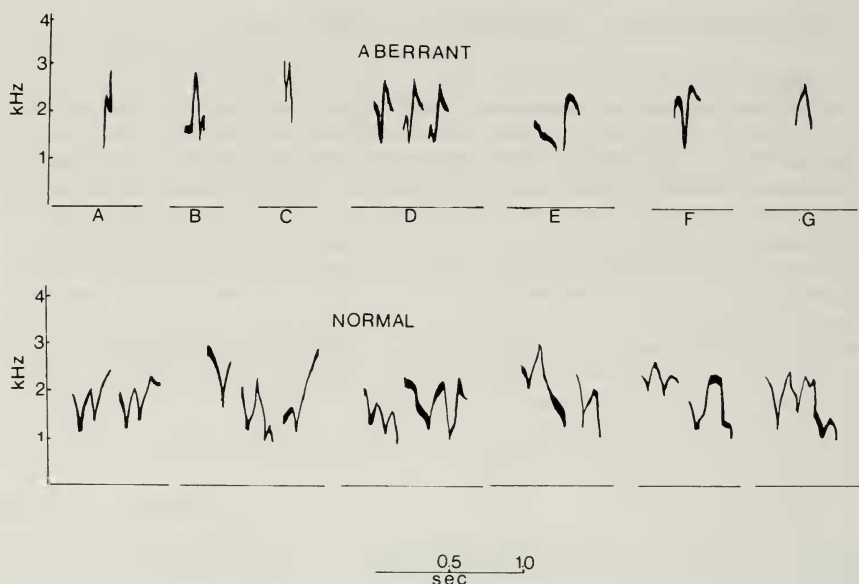


FIG. 1. Tracings of sonograms of the 7 phrases in the song of the aberrant vireo in June 1973 and 7 randomly selected normal phrases.

Results.—(1) The song. Lemon (1971) found that individual Red-eyed Vireos had repertoires of 40–60 elements, occurring either regularly in combinations or usually singly. Sequence rules for the elements and the combinations were not detectable, although extensive numbers of songs were analyzed.

Fig. 1 shows sonogram tracings of phrases of the aberrant vireo as well as some randomly chosen phrases from normal songs. The aberrant phrases are consistently shorter and less structurally complex than those depicted here or in Lemon (1971) or Rice (1978a). The 7 phrases represent all the phrases of the aberrant vireo during a 10-day recording period in June. When examined for sequencing rules, frequency of occurrence of the possible pairs of phrases deviated significantly from random (Table 1). Certain sequences, such as C-E and E-G, occurred more frequently than expected, and fewer pairs occurred than were predicted by the Poisson distribution.

(2) Playback experiments. When the playback stimulus is normal Red-eyed Vireo song scores are higher during experimental periods (test and post-test) than during pre-test control period in 11 of 20 cases (Fig. 2). Taking the response rate to normal song as a baseline rate for late June, the expected probability of an increase in response intensity during experimental periods is 0.55. After the aberrant song, 4 of 20 periods have higher scores than do their control periods (Fig. 2). The probability of obtaining a response rate this low or lower with a response rate of 0.55 is 0.002 (binomial expansion). The responses to this aberrant song by territorial vireos are significantly rarer than responses to normal Red-eyed Vireo song.

In the playback experiments with Red-eyed Vireos reported in Rice (1978a, b), 2 pre-test periods were measured during 79 trials. In these 79 trials, the response score during the second pre-test period had a 0.23 probability of being greater than the response score of the

TABLE I
TRANSITION FREQUENCIES AND GOODNESS OF FIT COMPARISON TO A RANDOM
DISTRIBUTION FOR THE PHRASES OF THE ABERRANT VIREO

Following phrase of pair	Preceding phrase of pair						
	A	B	C	D	E	F	G
A	—	1	0	2	1	2	2
B	4	—	0	1	1	1	3
C	4	1	—	1	0	1	4
D	0	3	0	—	1	1	0
E	0	0	11	0	—	0	0
F	0	4	0	0	2	—	0
G	1	1	0	0	5	2	—

Total of 62 phrases in 42 possible pairs of the phrases in Fig. 1 yield

No. times pair occurred	No. pairs	
	Expected from Poisson	Observed
0	9.60	17
1	14.17	12
2	10.46	5
3	5.14	2
4 or more	2.63	6

Chi square = 15.11, df = 4, $P < 0.01$.

first pre-test period. Using this as a control value for spontaneous increase in response behaviors, the probability of obtaining an increase in 4 or fewer of 20 paired 2-min trials is 0.499. The behavior of the vireos during playback of the aberrant song was not different from the behavior of vireos when no song was present. Clearly the vireos did not react to this aberrant song as if it were the song of a conspecific.

Several studies have demonstrated individual recognition of immediate neighbors (Weeden and Falls, *Auk* 76:343-351, 1959; Krebs, *Ecology* 52:2-22, 1971; Emlen 1971; Goldman 1974; Kroodsmma, *Condor* 78:87-99, 1976; and others). All of the experimental vireos had territories distant from that of the aberrant vireo. Therefore, we cannot definitively conclude that the aberrant song played no role in territorial defense because of the lack of response in the experiments. To examine this question further the experiments were repeated with the 4 immediate neighbors of the aberrant bird.

Eight responses to 8 exposures of normal song did not differ from 6 responses to aberrant song (Fig. 3). This may reflect the small sample size. However, in the 79 experiments cited earlier there was no response to normal song in 22 instances. Using that as a measure of the normal rate of nonresponse to conspecific song, a result of 6 or more responses in 8 trials has a probability of occurrence of 0.527. The neighboring Red-eyed Vireos appeared to react to the aberrant song no differently than they did to normal song. Also, their response frequencies were those of territorial Red-eyed Vireos (in general) to normal song. The aberrant song may have functioned to restrict incursions by close neighbors.

(3) Late song. By mid-July I felt that the song of the aberrant vireo more closely resembled normal song. Sonograms of tapes of the mid-July song revealed several changes (Fig. 4). The

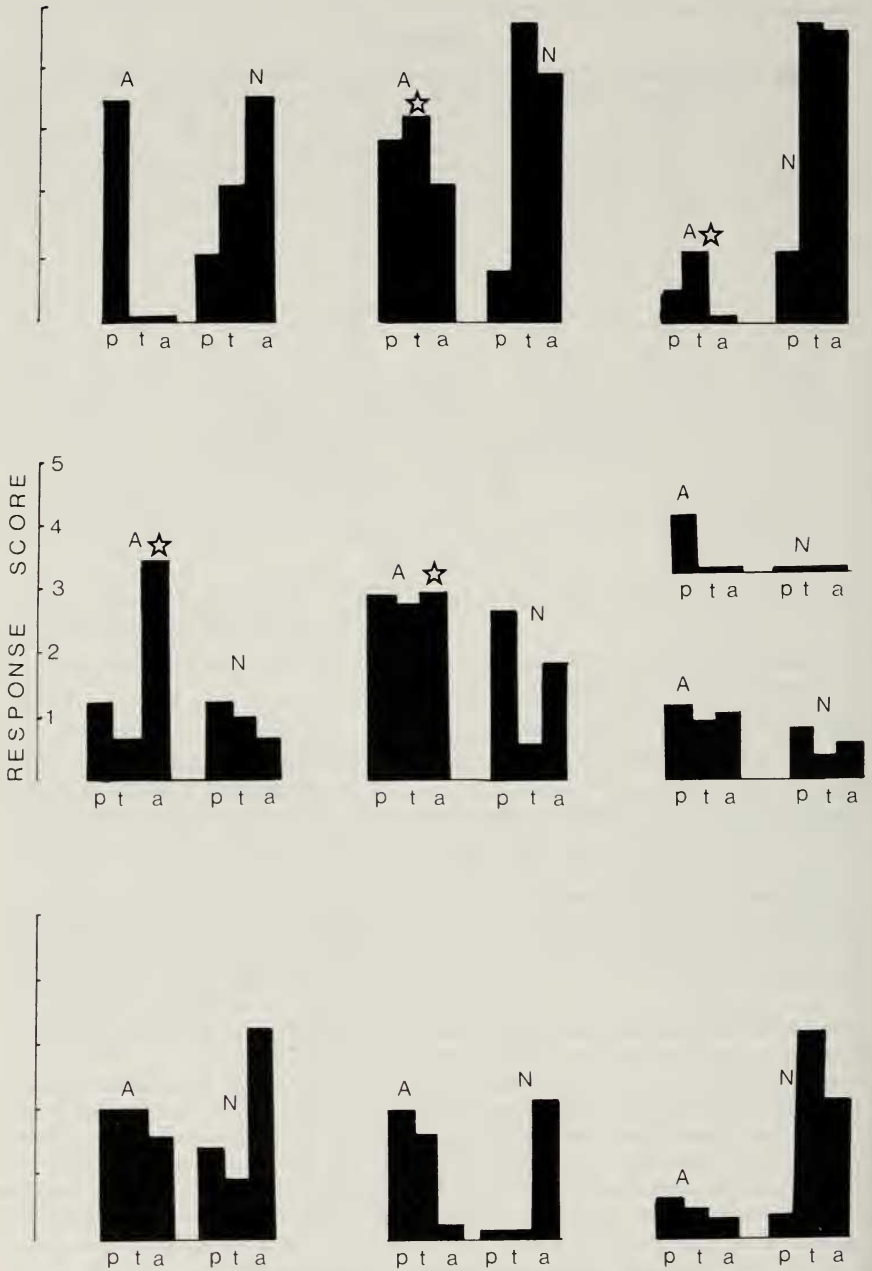


FIG. 2. Response scores for the experiments to non-neighboring territorial vireos, using aberrant (A) and normal (N) songs in June; "p" is the pre-test period, "t" the test period and "a" the post-test period; stars mark the cases where experimental period scores were higher than control period scores for tests with aberrant song.

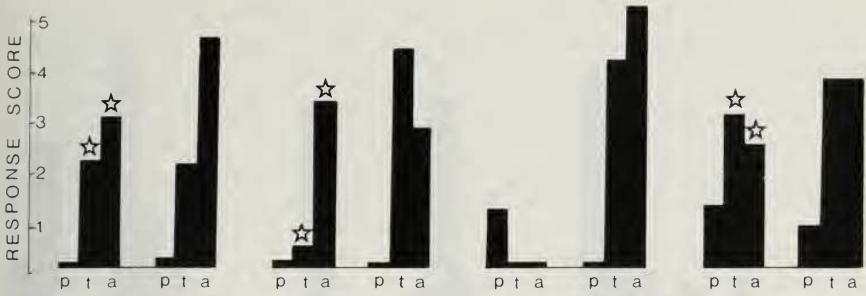


FIG. 3. Response scores for the experiments to neighboring territorial vireos using aberrant (first) and normal (second) songs. Symbols as in Fig. 2.

number of elements had increased slightly, with the addition of apparently new phrases (e.g., T) and possible differentiation of old phrases (e.g., E becoming U and Y, D becoming Z). The new phrases were more similar to those of normal Red-eyed Vireo song. The order of sequencing of phrases was also slightly less rigid than during June.

A second series of playback experiments with 9 territorial vireos was started on 14 July. By this date the rate and intensity of response to normal song is waning, but still responses can be fairly consistently elicited (Rice 1978b). The response scores of the vireos to normal song were greater in experimental than pre-test periods in 11 of 18 cases, giving a probability of response of 0.611 (Fig. 5). Increases in response scores to the late aberrant song occurred in 6 of 18 trials. With a response of probability of 0.611, 6 or fewer responses are expected with a probability of 0.02. The probability of observing the 6 or more responses under the rate of response to the earlier aberrant song is 0.14. Although the response rate has increased as predicted, the amount is not statistically significant.

(4) Natural encounters. In 39 h of observation between 14 June and 26 July 1973, I saw the aberrant vireo interact with other vireos 5 times. For other vireos with normal songs, in 125.5 h of observation over the same period, I observed 27 encounters. Also, there was no evidence of an increase in duration or intensity of encounters for the vireo with aberrant song, so the aberrant song did not make the bird appear less effective during natural encounters.

(5) Habitat quality. It is possible that this aberrant Red-eyed Vireo was occupying a territory effectively, but the territory was of inferior quality. I studied the habitat use of vireos



FIG. 4. Tracings of sonograms of the phrases in the song of the aberrant vireo in July 1973.

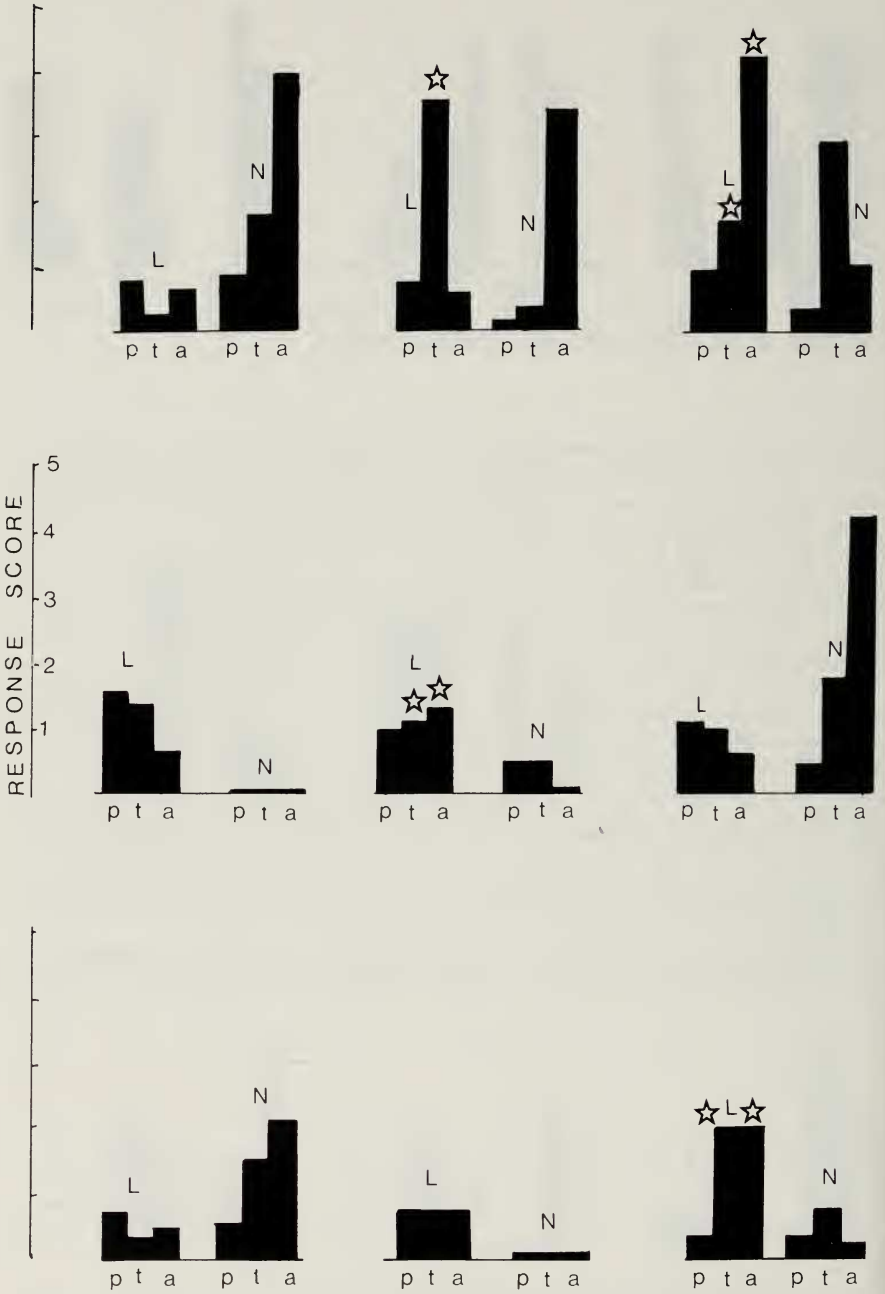


FIG. 5. Response scores for the experiments to non-neighboring territorial vireos, using late season (L) and normal song (N) from July. Symbols as in Fig. 2.

in this area in detail (Rice 1978c) and the vegetation on this territory seemed typical of most of the study area; a mature and entire aspen-white birch canopy and a fairly open alder-hazelnut understorey. Quantitatively, across 3 data sets representing species composition, foliage and height distribution, and occurrence of foraging sites, 18 principal components accounted for noteworthy amounts of habitat variability (see Rice 1978c for details). The Euclidean distance of this territory score from the centroid of all 72 Red-eyed Vireo territory scores is closer to the centroids than the scores of more than 70% of all territories for each data set. This means that quantitatively the habitat occupied by the aberrant vireo is similar to the habitats occupied by the other Red-eyed Vireos in this area.

(6) Breeding success. I was not able to find the nest of this aberrant vireo, but I did see the bird frequently with a nonsinging bird and observed a variety of social behaviors, including a swaying bout (Nolan, *Condor* 64:273–276, 1962; Barlow and Rice, *Can. J. Zool.* 55:528–542, 1977). From these observations I inferred that the aberrant bird was a male and had a mate which stayed on its territory until at least 25 July.

I frequently saw the bird and its presumptive mate feeding 2 Brown-headed Cowbird (*Molothrus ater*) chicks, but no vireo chicks. However, of 13 Red-eyed Vireo pairs in the areas whose fledging success I knew for 1973, 10 fledged only 1 (4 cases) or 2 (6 cases) cowbirds, and no vireos. Thus, although there is no support for the assertion that the aberrant bird was able to breed successfully, it was no less fit than three-fourths of the Red-eyed Vireos breeding in the area.

Discussion.—There are extensive data demonstrating that species-typical song plays an important role in vireo social behavior, particularly in inter-male aggressive encounters and courtship (Barlow and Rice 1977, Rice 1978a). However, it is clear from this study that in Red-eyed Vireos the singing of a species-typical song is not always essential for the establishment and maintenance of a territory, or for obtaining and keeping a mate. In other studies as well, birds with aberrant songs have paired and sometimes bred successfully (Baptista, *Z. Tierpsychol.* 34:147–171, 1974; Emlen, Thompson and Rising, *Wilson Bull.* 87:145–179, 1975).

It is certainly possible to find specific types of information encoded in specific aspects of a species-typical song or other social signal. However, it does not necessarily follow that in the absence of any specific aspect of a song the information cannot otherwise be readily conveyed. The cost of conveying information along these alternate channels (visual displays, call notes, etc.) may be higher, but data on this point are conspicuously lacking. This vireo had both a mate and a territory typical of Red-eyed Vireos in the area, implying that the costs were not excessive and/or the alternative channels not substantially poorer. Investigators using playback experiments must bear in mind that such studies can only demonstrate that a parameter is or is not sufficient for species (or individual) recognition, not that it is necessary. Possibly for behavioral functions as important as social activities (or orientation and navigation where multiple redundant cues are also common [Schmidt-Koenig, ed., *Animal Migration, Navigation, and Homing*, Springer-Verlag, Berlin, West Germany, 1978]) selection favors systems of multiple cues and responses. There is a need for studies providing realistic measures of the costs of such systems, relative to their possibly substantial benefits, including opportunistic studies of naturally occurring “experiments” such as the one reported here.

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Courtship feeding and copulation of Royal Terns.—Although mentioned by Buckley and Buckley (Ibis 114:344–359, 1972) in their paper on the nesting of Royal Terns (*Sterna maxima*), courtship feeding and copulation have not been described for this species. These performances may occur on beaches away from islands used for nesting (Kale et al., Bird-Banding 36:21–27, 1965). Such breeding activities were apparently performed off site by the terns I studied on Cabretta and Sapelo, tree-covered islands in Georgia where they have never been known to nest. Royal Terns have, however, nested on Little Egg Island 3–10 km away (Kale et al. 1965).

My studies were made from 18–28 April 1979. It was difficult to quantify all phases of behavior since the terns were crowded in groups of from 20–200 or more, resting and preening at the water's edge.

Males, carrying a fish crosswise in their bills and making *kur-itt*, *kur-itt* notes, initiated courtship feedings by flying low over the flock, apparently to locate and alert their mates, possibly by individually recognizable "fish calls" described by Hutchinson et al. (Behavior 32:150–157, 1968) for the Sandwich Tern (*S. sandvicensis*). Transfers of fish took place in 3 situations. (1) Transfers occurring within the crowd of other terns were noted 8 times, but were interfered with twice by other terns and twice by Laughing Gulls (*Larus atricilla*) that rested among them. In the other 21 feedings or attempted feedings, the birds which were considered female (because they received food) either (2) walked out from the crowd or (3) flew to an empty part of the beach 5–10 m away.

Both birds displayed, with necks extended upward and the fore part of the closed wings held outward (Fig. 1). The female stood lower than the male, snatching the fish so quickly that display was often only momentary. The size of the fish offered appeared to be important to female selection. On 23 occasions in which the female accepted, the fish was about 7 cm in length. Of 7 refusals observed, 4 times in succession by 1 female, the fish was 5 cm in length or less and slender. When 1 male offered his mate a small fish and was refused, he walked over to offer the fish to a neighboring tern. This tern, sex undetermined, also refused. The male then returned and after several tries mounted his mate, swallowing the fish as he did so. Full copulation followed. This was the only time I observed any relation between courtship feeding and copulation.

Sometimes males and females flew to dip their bills in the waves 2–4 times. Afterwards, males flew to sea and females returned to the flock. One pair fed, then walked together in full display to the water's edge and dipped their bills in a mixture of wet sand and water 6–8 times.

Copulatory or pre-copulatory behavior, with one or more pairs performing, was so common as to be almost continuously occurring in larger flocks. Displays preceded copulations. The male, with neck extended and slightly back, and the bends of wings out like a skirt (Fig. 1), tried to walk around the female who kept turning. She often started in a low resting pose, assuming the display only as the time of mounting approached. The male held his head higher than hers, pointing his bill downward. Copulations lasted 50 sec–4 min. During nearly all of this time, males merely stood on the shoulders of the females, flapping their wings to